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Earliest evidence for the structure of *Homo sapiens* populations in Africa

Eleanor M.L. Scerri [a,*], Nick A. Drake [b], Richard Jennings [c], Huw S. Groucutt [c]

[a] PACEA, Université de Bordeaux, Bâtiment B19, Avenue des Facultés, 33405 Talence Cedex, France
[b] Department of Geography, King's College London, K4U.06 Strand Campus, London WC2R 2LS, United Kingdom
[c] School of Archaeology, Research Laboratory for Archaeology and the History of Art, University of Oxford, 28 New Barnett House, Little Clarendon Street, Oxford OX1 2HU, United Kingdom

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ABSTRACT

Understanding the structure and variation of *Homo sapiens* populations in Africa is critical for interpreting multiproxy evidence of their subsequent dispersals into Eurasia. However, there is no consensus on early *H. sapiens* demographic structure, or its effects on intra-African dispersals. Here, we show how a patchwork of ecological corridors and bottlenecks triggered a successive budding of populations across the Sahara. Using a temporally and spatially explicit palaeoenvironmental model, we found that the Sahara was not uniformly ameliorated between ~130 and 75 thousand years ago (ka), as has been stated. Model integration with multivariate analyses of corresponding stone tools then revealed several spatially defined technological clusters which correlated with distinct palaeobiomes. Similarities between technological clusters were such that they decreased with distance except where connected by palaeohydrological networks. These results indicate that populations at the Eurasian gateway were strongly structured, which has implications for refining the demographic parameters of dispersals out of Africa.

1. Introduction

The time depth and spatial organization of early *Homo sapiens* population substructure within Africa have been only minimally explored, but both play a critical role in explaining modern human origins. This is because a number of different early demographic events and processes in Africa could have generated the character of human genetic diversity observed today (Nielsen and Beaumont, 2009). As a result, models of early *H. sapiens* dispersal are often conflicting (Endicott et al., 2009; Soares et al., 2009; Scally and Durbin, 2012; Mellars et al., 2013). In the absence of ancient DNA, attempts to clarify the demographic organization and structure of African populations prior to range expansions into Eurasia have focused on understanding intra-African dispersals during the Middle Stone Age (MSA, ~280–30 ka). These studies include perspectives from different sources of data, which have each emphasised different evolutionary processes and empirical limitations (McBrearty and Brooks, 2000; Atkinson et al., 2009; Gunz et al., 2009; Blome et al., 2012) (See Supplementary Information 1, or SI 1). However, reconciling these factors to produce more integrated analyses relies on the ability to bypass problems of data compatibility and resolution.

Palaeoclimatic research has played a critical role in providing a framework for combining different types of evidence (Blome et al., 2012; Ziegler et al., 2013) In particular, significant research on a 'Green Sahara' (i.e. the Sahara when it was environmentally ameliorated due to increased water availability) has postulated that between ~130 and 75 thousand years ago (ka), there was no barrier to modern human dispersal out of sub-Saharan Africa (Drake et al., 2011; Blome et al., 2012; Coulthard et al., 2013; Larrasoaña et al., 2013). Extensive evidence of humid conditions in the Sahara has been linked with the dispersal of large, savannah-adapted mammals and the appearance of new stone tool (lithic) industries in the region (McBrearty and Brooks, 2000; Geraads, 2010; Drake et al., 2011) (SI 1). However, this provocative evidence is still circumstantial. As a result, the character of dispersal and its articulation with the spatial structure and variation of populations in this critical region between sub-Saharan Africa and Eurasia is still unknown, limiting inferences of early *H. sapiens* demography.

This is the case for several reasons. The extent of the 'Green Sahara' is currently controversial. Larrasoaña et al. (2013) suggest

* Corresponding author.
E-mail address: eleanor.scerri@u-bordeaux.fr (E.M.L. Scerri).

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that when the Sahara underwent environmental amelioration, the entire desert was transformed into savannah and grasslands. In contrast, the continual presence of arid pollen in cores off the Northwest African coast since Marine Isotope Stage (MIS) 16 indicates that regions of desert always existed within the Sahara (Hooghiemstra et al., 2006). This is further supported by the presence of arid adapted species that have been able to survive and evolve in the Sahara since the onset of the desert about 7 million years ago (Metallinou et al., 2012; Šmíd et al., 2013). Secondly, determining the extent of a 'Green Sahara' and its effect on human dispersal is compounded by a lack of understanding of the relationships between the ecology and archaeology of North Africa between ~130 and 75 ka ago (MIS 5) (Drake et al., 2011). Research at various broadly contemporary sites across North Africa has indicated that human populations in the region were associated with a range of different environments (Smith et al., 2004; Geraads, 2012; Jacobs et al., 2012). The degree of variation between North African MIS 5 lithic technologies is itself also contentious. Apparent technological facies and traditional differences between named industries obfuscate often confusing and interchangeable nomenclatures that lack clear definitions (Wendorf et al., 1987; Vermeersch, 2001). These industrial units have been defined on inconsistent grounds, with retouched tools largely defining the Aterian, but high frequencies of a particular core reduction method for defining the Nubian Complex. Other research has instead indicated the presence of a constellation of related and overlapping technological features in assemblages across North Africa (Bouzouggar and Barton, 2012; Dibble et al., 2013; Scerri, 2013a; Spinapolice and Garcea, 2013), but no large-scale technological comparison has been conducted to conclusively resolve these issues (SI 1).

In this paper, we therefore study and integrate archaeological and palaeoenvironmental data from across MIS 5 North Africa. The morphological and technological diversity of lithic assemblages was analysed in relation to a new model of the spatial extent of major biomes combined with the location of palaeohydrological resources. This allowed the ecology and hydrology of North Africa during MIS 5 to be linked for the first time with archaeological data to explore intra-African dispersals and its effect on the structure and variation of early *H. sapiens* populations.

2. Materials and methods

2.1. Palaeoclimate model

The MIS 5 biome model for the Saharo-Arabian arid belt was generated from temperature and rainfall data that was acquired from a downscaled version of the Community Systems Model (CCSM 3) (Hijmans et al., 2005). The use of downscaled climate data means that the model has a cell resolution of 30 arc seconds (c. 1 km), which is significantly higher than the 2.5-degree cell resolution of standard global climate models. This raster data was reclassified and combined into a series of biomes using ESRI ArcGIS 10.1 geographic information system (GIS) software. Climatic parameters of the biomes were generated from the result of a correlation of present day global temperature and rainfall values with the World Wildlife Fund (WWF) for Nature biome map (Olson et al., 2001). This involved classifying mean annual temperature values into eight classes of 5-degree intervals (ranging from −30 °C to 30 °C) and combining them with seven annual precipitation intervals (hyper-arid <100 mm; arid 100–200 mm; semi-arid 200–300 mm; dry 300–600 mm; sub-humid 600–1000 mm; humid 1000–1600 mm and hyper-humid >1600 mm). The 56 resulting permutations were assigned a biome category from the WWF map based on the dominant biome per permutation. These categories were then applied to the LIG model temperature and rainfall values. The Biome map was then overlaid with a map of the palaeohydrology (Drake et al., 2011) within a GIS framework.

2.2. Lithic analyses

The second stage of the study compared lithics sampled from 17 temporally and spatially representative lithic assemblages from across North Africa (Fig. 1, Table S1) (SI 2). These assemblages are known variously as 'Aterian', 'Mousterian' and 'Nubian Complex', wider assemblage groups or industries that have been associated with *H. sapiens* skeletal remains (SI 1). The sample also includes an additional control group from the Arabian Middle Palaeolithic (SI 2). These comparative analyses aimed to understand the diversity of technological behaviours present in the sample and link these to different sources of variability. This is because lithic technology and morphology are cross-cut by a number of constraints. However, there is general agreement that learned (i.e. cultural) dimensions of technological behaviour reside in patterns of residual variability that cannot be explained by pragmatic factors such as raw material availability, function and/or mobility strategies (Foley, 1985; Winterhalder, 1986; Mithen, 1989; Van Peer, 1991; Broughton and O'Connell, 1999; Ingold, 2000; Foley and Mirazón-Lahr, 2003; Kuhn, 2004; Bird and O'Connell, 2006). These residual 'cultural' traits can broadly be defined as constellations of shared, learned behaviours, and at the scale of analysis relevant to this study, it is the pattern of differentiation between these constellations that is of interest (Collard and Foley, 2002; Henrich and McElreath, 2003; Foley and Mirazón-Lahr, 2011). This is because, at a biogeographic level, the diversity of culture has been correlated with the dynamic feedback between cultural and ecological systems, particularly in relation to hunter-gatherer societies (Nettle, 1998; Collard and Foley, 2002; Currie and Mace, 2012). Accordingly, patterns approximating demic organization will be apparent within the orthogonal variability of the goodness-of-fit between environmental conditions and relevant dimensions of technological variation.

The lithic sample formed a database of >300,000 attribute measurements reflecting various knapping actions taken along the production continuum (SI 3). At a basic level, lithic reduction is a directional and irreversible process characterized by mechanical relationships affected by their place in this process (Hovers, 2009; Tostevin, 2013). These mechanical relationships, which vary according to their temporal place in the sequence, result in various attributes that can be quantified from the perspective of cores, flakes and tools (SI 3). In this way, independent, equivalent mechanical or technological relationships can be compared between assemblages, each representing an individual, quantifiable measure of relatedness and a different information pathway (see SI 3). Depending on their variation and their spatial distribution amongst other factors, the nature of these technological relationships can in this way be linked to different constraints and behaviours, for example such as risk, cost, design and efficiency (Torrence and van der Leeuw, 1989; Winfrey, 1990; Jeske, 1992; Bleed, 1996). In this paper, we assess the structure of these different pathways and their covariance with ecological variables in order to reveal patterns approximating the organization of different demes in North Africa during MIS 5 (SI 3).

Our inferences are drawn from the character of variability between these technological relationships for each of the three classes of lithics using multiple principal components (PCA) and correspondence analyses (CA). Multivariate and regression analyses are first performed to determine the effects of contextual information such as raw material type, distance and the degree of technological reduction intensity on the comparability of

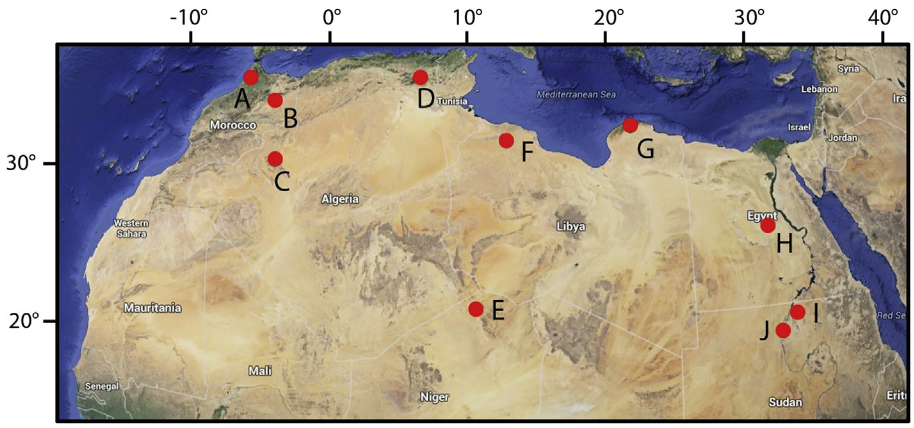

Fig. 1. Archaeological sites used in the study. A: Mugharet el Aliya and Grotte des Contrebandiers (Morocco); B: Krenoussa (Morocco); C: Tabelbala (Algeria); D: Bir el Ater (Oued Djebbana) and Bir Chaacha; E: Adrar Bous (Niger); F: Wadi Gan (Libya); G: Haua Fteah (Libya); H: Bir Tarfawi 14; Kharga Oasis, 8708, 8735, 8751; I: 1010–8; 1033; J: Sai Island. Base map courtesy of Google Earth.

assemblages, in order to inform and optimize the reliability of interpretation (SI 3). We then compare relevant PC scores for each analysis between assemblages using ANOVA to obtain an overall structure of technological similarities and differences for all three classes of lithics, without bias from industrial nomenclature. These overall results were then integrated with the climate model (see Section 2.3 below).

The units of analysis (i.e. attributes on lithic artefacts) were selected to reflect interdependent clusters of knapping actions that together form mechanical relationships which have been shown through experimental knapping to be independent (e.g. Speth, 1972, 1974; 1975; 1981; Dibble and Whittaker, 1981; Cotterell and Kamminga, 1990; Pelegrin, 1990, Chazan, 1997; Dibble, 1997; Pelcin, 1997a; 1997b; 1997c; 1998; Dibble and Rezek, 2009; Rezek et al., 2011) and follows an approach first designed by Tostevin (2013). The selection of attributes is therefore also based on experimental knapping studies. Each attribute is described, together with its attribute states and measurement descriptions in SI 3. Raw data was first normalised using Box-Cox Transformations. We used multiple Principal Components and Correspondence Analyses to

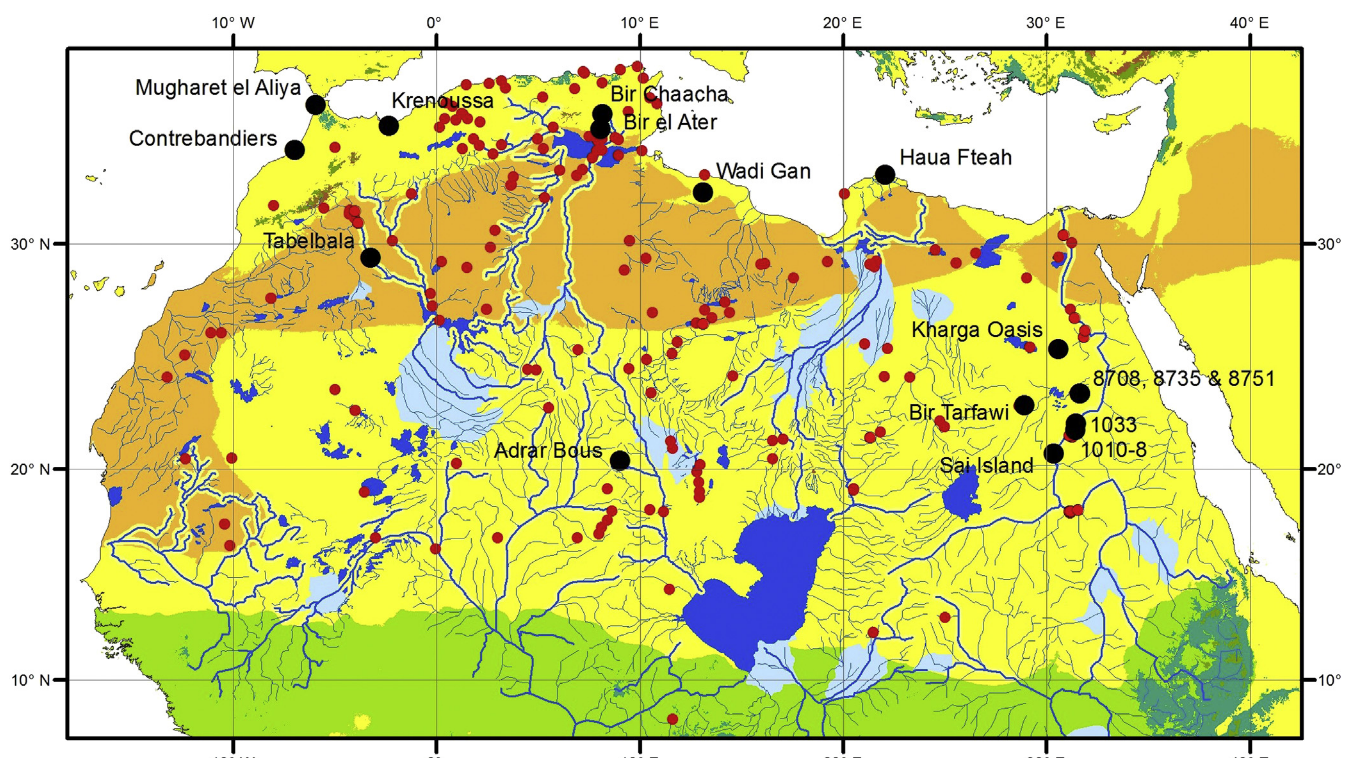

Fig. 2. MIS 5 Biome Model of North Africa with the locations of MSA sites, including archaeological sites sampled for analysis. Yellow: savannah grassland and shrubland; orange: desert belt and xeric shrubland; light green: rainforest; dark green: broadleaf/coniferous forest. Pleistocene lakes (dark blue), river networks (blue), alluvial fans (light blue), sample sites (black) and other MIS 5 archaeological sites (red) are also highlighted. The map shows that savannah grasslands, lakes and riparian corridors neatly explain the presence of numerous human occupation sites across North Africa in MIS 5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

explore the organisation of groups of attributes representing independent phases of tool manufacture, as reflected on cores, flakes and retouched tools. We compared bootstrapped component scores between assemblages using ANOVA after testing for equal variance between samples using Minitab 16 and PAST statistical software. We used R to generate heatmaps.

2.3. Model integration

Inverse Distance Weighted spatial interpolation tools in ArcGIS 10.1 Spatial Analyst Extension were used to convert the multiple ANOVA results of the lithic analyses into surface or heat maps. The processing extent was set at 10°–35° longitude and from −18° to 40° latitude. The resulting maps were then integrated with the MIS 5 biome model within a GIS framework.

3. Results

3.1. Climate model

We generated the spatial extent of major ecosystems or biomes in North Africa for early MIS 5 (~130 ka), when the environment was more humid than today (Fig. 2). The model shows that the Saharo-Arabian desert belt contracted to between 28° and 30° N across North Africa during this time, with the exception of the continuation of desert between 17° and 30° N along the west coast of Africa. The advancement of the African Monsoon System to 28° N from its current maximum extent of 18° N explains the contraction of the desert and the advancement of subtropical savannah grasslands. These grasslands are inferred from annual precipitation values, which ranged from 300 to 600 mm (dry) in the model compared with <200 mm (arid) in the same area today. The increased precipitation simulated by the climate model not only transformed the biomes for North Africa but would also have activated the lakes and river systems.

The integrated palaeohydrology shown in Fig. 2 also illustrates that the Sahara had a dense network of rivers and lakes. The articulation between this hydrological network and the modelled biomes shows how previously uninhabitable regions became environmentally ameliorated and how dispersal was possible even across the arid belt. The Niger, Chari and Nile to the south and the rivers draining the Atlas Mountains in the north have headwaters outside the desert, providing refuges for biota during arid periods and riparian dispersal routes into the Sahara during humid periods. Numerous hydrological systems also fed water from the central Saharan mountains in all directions (Figs. 2 and 3). Three of these large rivers captured monsoon rainfall during humid periods, when the rainfall reached a northerly position, and transported it northwards across the desert barrier identified by the palaeoclimate model (Fig. 2). The Irharar and Serir Tibesti Rivers transported waters into the Mediterranean while a large river emanated from the western flanks of the Hoggar Mountains and flowed into the Ahnet-Mouyder Basin. In this basin, the river joined with the Soura River, which flowed south from the Atlas Mountains. These combined waters formed the Ahnet-Mouyder Megalake that existed during MIS 5 (Conrad, 1969) (Figs. 2 and 3). The River Nile provided a further corridor, though in this case the waters were derived from tropical East Africa. The Nile could have formed a corridor across the desert during periods when the Sahara desert was large but East Africa humid, as is the case today. Thus, it is

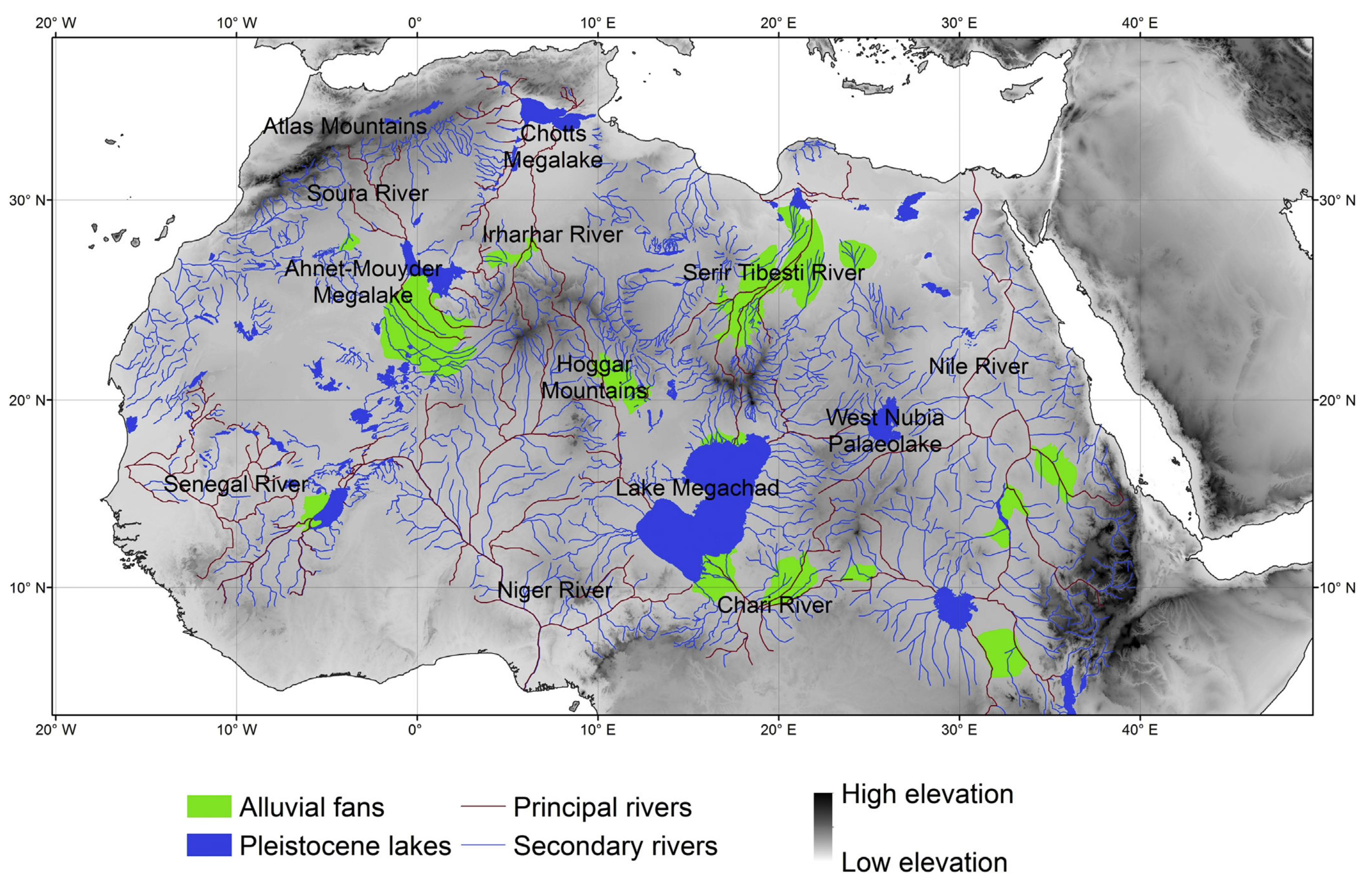

Fig. 3. Topography of North Africa with the paleohydrology of MIS 5 overlain. The hydrological systems that form connections throughout the Sahara are shown in brown, in order to highlight them. The alluvial fans that in some cases allow interconnections between river systems are also displayed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

possible for this riverine corridor to be active when the others are dormant. However, it is known to cease running during periods when both the Sahara and East Africa experience low rainfall, as was the case for much of the last glacial period (Revel et al., 2010).

Analysis of West African palaeohydrological and palaeobotanical records suggests that similar conditions to those we have modelled in MIS 5 existed in the Sahara during the Holocene humid period (Hély and Lézine, 2014). This analysis supports the utility of our model and the presence of the arid belt at 28° N. Hély and Lézine (2014) classified pollen taxa according to their phytogeographical affinities, recognising four groups adapted to increasingly humid conditions (Saharan, Sahelian, Sudanian and Guineo–Congolian) in the present-day Sahara and to the south of it. Results revealed that the taxa of the Sahel, equivalent to an arid savannah, exhibited a rapid northern expansion to 27.5°N by 9 ka at the expense of Saharan vegetation. In MIS 5, savannah characterised by Sahelian taxa expanded to a similar latitude (Fig. 2). Taxa from the Sudanian region, which is equivalent to a humid savannah, also expanded, reaching a maximum northward extent of 25°N at a similar time. Similarly, Guineo–Congolian vegetation moved north, but this phytogeographical group did not migrate as far, reaching about 18°N. This latter group is equivalent to our rainforest biome that reached 14°N during MIS 5, thus suggesting that there were some differences in vegetation distributions between the Sahara in the Holocene and MIS 5.

The region occupied by the early Holocene Sudanian expansion coincides with the maximum extent of Holocene lacustrine and palustrine hydrological records. Hély and Lézine (2014) conclude that the most likely reason for the relationship between palaeobotany and palaeohydrology is that riparian forests developed along rivers and lake/wetland shorelines. These rivers are thus likely to have provided preferential dispersal routes for plants (and animals) into the Sahara at the start of the Holocene wet phase, just as we propose for the Sahara during MIS 5.

While these hydrological connections allowed animals and *H. sapiens* to disperse across the east-west Saharan arid belt we identify during MIS 5, our research also suggests that these riparian corridors created spatial and ecological bottlenecks that may have potentially hindered the dispersal of some taxa, particularly if other competing animals already occupied the available ecological niches in the region. Faunal evidence supports this view. For example, during the early Holocene humid period only those fish that exhibited adaptions allowing them to cope with ephemeral water bodies managed to disperse across the Sahara using routes other than the Nile (e.g. the Redbelly tilapia, *Tilapia zillii*, and the African sharptooth catfish, *Clarias gariepinus*), indicating that the flow of these Saharan rivers was seasonal (Drake et al., 2011). Animals adapted to more permanent and deeper water conditions (e.g. Nile Perch, *Lates niloticus*, and the Hippopotamus, *Hippopotamus amphibious*) only migrated as far as the central Sahara at about 26°N (Drake et al., 2011), where plentiful monsoon rainfall created permanent water bodies. Notwithstanding the lack of water in the northern Saharan rivers during the dry season, they allowed a selection of savannah animals such as Elephant and Giraffe to disperse across the arid belt and colonize the more humid region to the north (Drake et al., 2011) (Fig. 2). Savannah animals also appear to have crossed the Sahara during MIS 5, presumably in a similar manner. Fossil evidence indicates that the giant buffalo *Pelorovis antiquus*, and the hartebeest *Alcelaphus buselaphus* dispersed across the region from East Africa to the Maghreb (Geraads, 2010). Molecular phylogenetics indicates that this east-west dispersal was also the case for the common genet *Genetta genetta* and the cheetah *Acinonyx jubatus*, thus providing evidence for biological connections at this time (Gaubert et al., 2009; Charruau et al., 2011).

Critically, our model shows that, whilst the savannahs opened up large areas of the previously hyper-arid Saharan landscapes for dispersal, they restricted trans-Saharan dispersal to four large riverine/lacustrine corridors that cross this arid belt. These bottlenecks limit the number of regions that could be crossed and ecological niches that could be colonized, thus filtering dispersal both spatially and ecologically.

3.2. Technological analysis

Multiple multivariate analyses (Methods, SI 3, SI Tables S2–S8) of the technological relationships exploited along the reduction continuum indicated the presence of a number of technological clusters that were strongly predicted by distance, rather than industrial nomenclature (Fig. 4). The degree of overlap between these

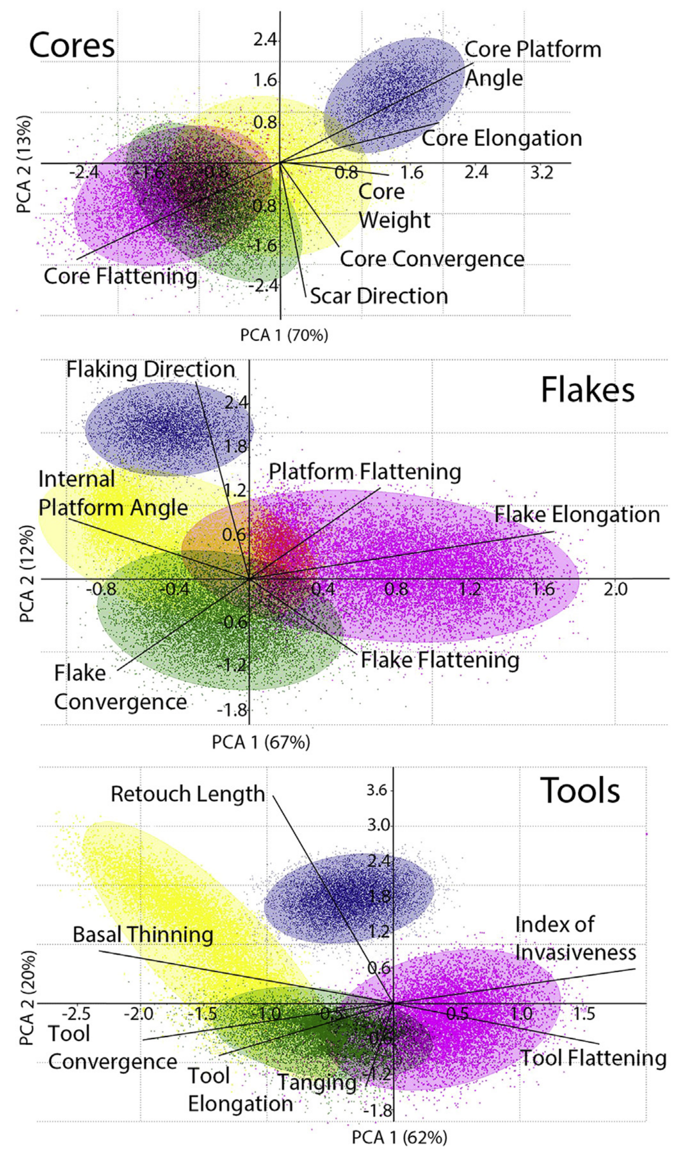

Fig. 4. Principal Components Analysis results for Core Exploitation analysis (top), Flake Platform Analysis (centre) and Tool (base) hafting morphology analysis using 95% data capture ellipses and coloured by region. Blue: control assemblage; yellow: northeast Africa; green: Sahara; pink: northwest Africa. Overlap between regions decrease from cores to tools. Results of all the multivariate analyses are summarised in Fig. 5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Main differences between assemblage groups in northwest, northeast and southern North Africa.

Northwest Africa	Northeast Africa	Southern Sahara
• Bifacial Foliates • Nubian Levallois technology decreases towards the Atlantic coast • Small Levallois cores • Shouldered, tanged and basally thinned tools • Convergent Levallois cores • Regular Retouch • Ovoid flakes • Small tanged convergent and side retouched flakes • High levels of retouch • Invasive retouch • Relatively higher Levallois index to other regions in North Africa	• Bifacial lanceolates • Nubian Levallois technology • Small Levallois cores • Core Axes • Shouldered, tanged and basally thinned tools • Denticulates and notches • Resharpening by burination • Laminar flakes • Medium sized tanged flakes with no active edge retouch • Retouch is not invasive	• Bifacial foliates & lanceolates • Nubian Levallois technology • Small Levallois cores • Core Axes • Shouldered, tanged and basally thinned tools • Denticulates and notches • Laminar and ovoid flakes • Small and thin intensively retouched tanged points • Very large tanged tools and elongated points • Invasive retouch

technological clusters was most pronounced for cores. Significant technological equifinality was observed between cores, indicating a commonality of core reduction across North Africa as well as a high degree of correspondence with reduction intensity (Fig. 4, Figs. S1–S2). Notwithstanding this substantial overlap, there were some general differences between northeast and northwest Africa, which is not unexpected given the distances between the two sub-regions of North Africa. The control group formed a markedly different cluster to the North African samples.

Multiple multivariate analyses of the various stages of flake production and their role in the process (e.g. core management flakes, preferential flakes) each indicated that flakes were organized into more distinct technological constellations, demonstrating a much smaller degree of overlap between northeast Africa, northwest Africa and the central Sahara (Fig. 4, Fig. S3). These results are compelling because, unlike cores, which reflect the terminal phase of reduction, the flake population reflects reduction throughout the process of manufacture. The results also indicate that diverse raw material constraints (e.g. raw material type, clast size, distance to source) were overcome to produce products that are distinctive enough to group into multivariate clusters, which correlate with sub-regions of North Africa. Identical analyses were conducted for the retouched tool sample in order to determine the presence of any differences in the selection of flakes for retouch. The results exhibited the same clusters. The same trends were observed again for the study of tool morphology, which included analyses of tool edge retouch, backing and hafting modifications (Fig. 4, Figs. S4–S5). Significantly, the technological clusters for the tool analyses were even more marked than they were for the analyses of flakes, indicating an even greater degree of distinction. These technological clusters do not correlate with industrial assignation and instead break down such traditional nomenclatures and apparent 'facies' (SI 1). Analysis of the orthogonal sources of variability driving our results instead permitted us to determine the main character of technological differences and their spatial organization, irrespective of assemblage classification (Table 1).

In order to test the interpretation that the multivariate descriptive statistics reflect regional divisions and understand them in more detail, we first compared the similarities between assemblages through ANOVA of the scores of each multivariate test result (SI 3). Summary results of test means are shown in Fig. 5, and separate boxplots and details for each test are shown in SI Tables S9–S12. While maintaining the broad regional divisions identified, these analyses also indicate more complex degrees of similarity and difference. In particular, Tabelbala, a northwestern site, sometimes clustered with sites hundreds of kilometres away in the central Sahara (Figs. 1 and 5). This was also the case for Adrar Bous, which showed strong similarities both with Tabelbala as well as Sai Island and other northeast African sites. Haua Fteah, appeared rather more distinctive, clustering with no northeast African assemblages but showing some weak similarities to them instead. Wadi Gan, broadly equidistantly located between northeast and northwest Africa, showed similarities to northwest Africa, a region to which it is connected by the savannah biome, but significant differences to northeast African sites, presumably due to the arid region in the Gulf of Sirte that separates these two regions.

3.3. Integrated analysis

The ANOVA scores summaries in Fig. 5 were integrated with the climate model shown in Fig. 2 in order to show the articulation of

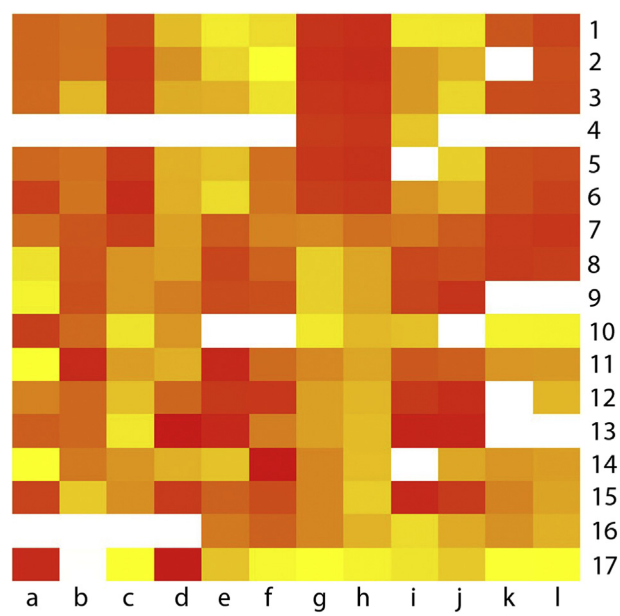

Fig. 5. Heat map summarizing the means from individual ANOVA (x axis) by assemblage (y axis). Similarity in colour in each vertical column represents the similarity of assemblages. Individual box plots with additional test information is shown in SI Tables S10–S13. White squared indicate missing data, where only certain artefact classes were available for study. Legend: a. blank dimensions; b. blank core exploitation; c. blank dorsal surface; d. blank platforms; e. tool core exploitation; f. tool dorsal surface; g. generic tool morphology; h. hafted tool morphology; i. tool platforms; j. tool dimensions; k. core management; l. core exploitation; 1. Mugharet el Aliya; 2. Contrebandiers; 3. Wadi Gan; 4. Bir el Ater; 5. Bir Chaacha; 6. Krenoussa; 7. Tabelbala; 8. Adrar Bous; 9. Sai Island; 10. Bir Tarfawi 14; 11. Kharga Oasis; 12. 1033; 13. 1010–8; 14. 8735; 15. 8751; 16. 8708; 17. Haua Fteah. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

technological variability with the ecology of North Africa during MIS 5. Summary results are shown in Fig. 6. The results both validate and provide an explanation for the highly structured and complex spatial organization of the multivariate technological clusters summarized in Fig. 5. Technological clusters correlate with discrete biomes in the climate model, showing how dispersal across the region could have taken place, but also why it was limited and fragmented, allowing differentiated technological traditions to develop in different regions. Crucially, the specific organization of similarities between the assemblages also shows a high degree of spatial structure, such that similarities are generally the greatest either with geographic proximity or when connected by riverine corridors. In north-central North Africa, a savannah biome belt connects Wadi Gan with other sites in the northwest. Tabalbala, to the south of the northwest cluster, is within an arid zone but connected to both the northwest and the savannah biome of the southern Sahara via a riparian/lacustrine corridor, explaining the similarities between this site and Adrar Bous, as well as Adrar Bous' similarities to sites in the Maghreb. Adrar Bous and other sites in the northeast are all part of the same savannah belt which is now occupied by the Sahara desert. This region is also characterized by the above-mentioned interlinking Nile, Chari and Niger River systems, thus facilitating dispersal along these corridors and explaining its similarities to these sites despite the distances involved. On the other hand, it is clear that Haua Fteah was separated from the other northeast African sites by an arid belt. The weak similarities between this site and others in the northeast may also be explained by riparian connections across the arid belt. The differences are interpreted as a reflection of the limited capacity of the Saharan riverine routes when crossing the desert belt. The

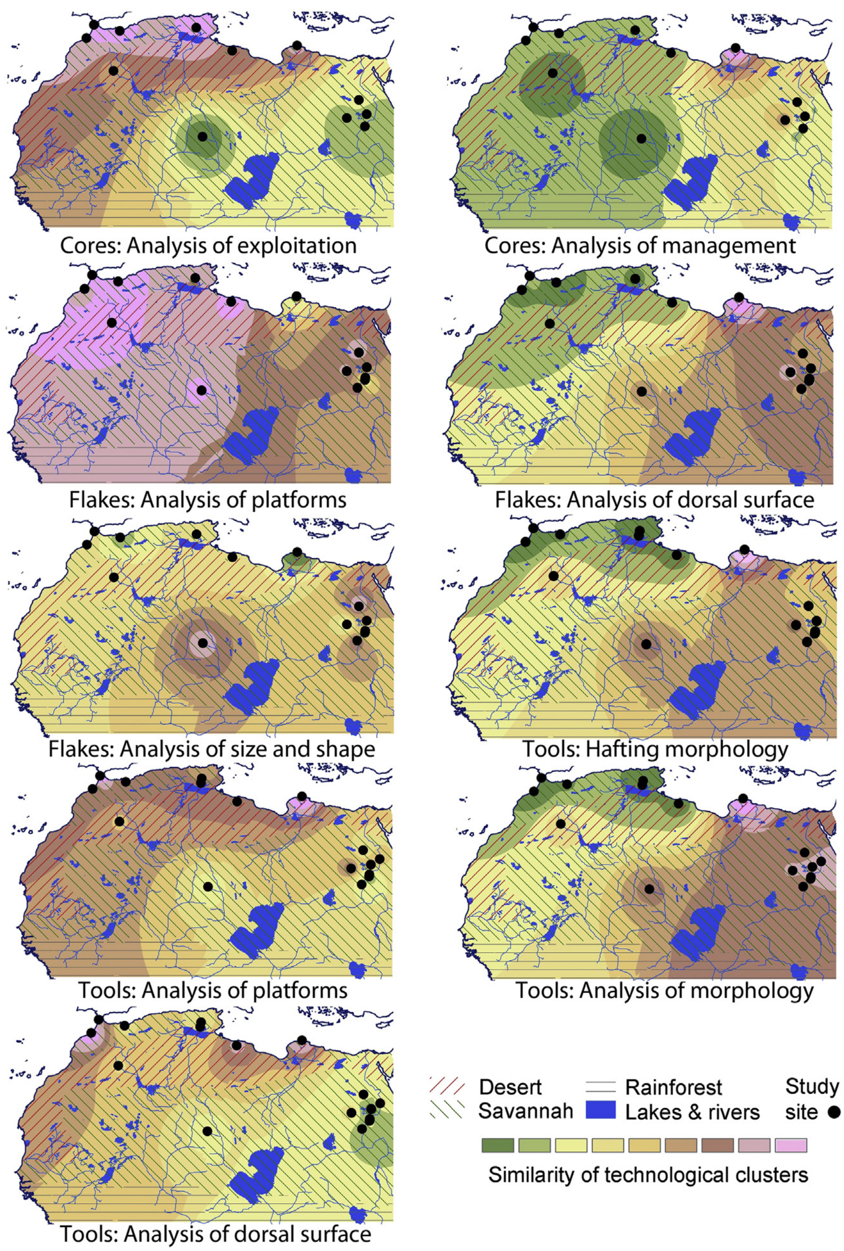

Fig. 6. Spatial interpolations of the ANOVAs of the Principal Components and Correspondence Analyses scores for core, blank and tool analyses, mapped in association with major modelled biomes and palaeohydrological networks. See SI Tables S2–S8 for full details of attribute measurements and SI Tables S9–S12 for detailed ANOVA results.

impact of seasonal, decadal and millennial differences upon limited and/or less stable riverine routes may have enhanced population isolation, leading to relative cultural isolation. This very specific pattern of technological similarity and difference also appears to be mirrored in the flora and fauna of the Jebel Akhdar (see discussion).

4. Discussion

Our combined results have reconciled the contradictory evidence for a 'Green Sahara' and shown how a patchwork of different biomes and palaeohydrological connections drove a distinctive budding of populations of *H. sapiens* across North Africa between ~130 and 75 ka. The integrated model indicates that these specific ecological and hydrological conditions and associated dispersal patterns triggered the formation of highly structured *H. sapiens* populations as well as a suite of technological innovations unique to the North African MSA (SI 1). The organisation of these technologies was more diverse than has been suggested by the traditional nomenclatures used to define them. Terms such as 'Aterian' or 'Nubian Complex' do not adequately reflect patterns and processes of adaptation, mobility and interaction, although they are useful heuristics for denoting assemblages featuring particular techniques, such as tang hafting or high frequencies of Nubian Levallois reduction. Such heuristics may play a useful role in attempting to understand the relationship between features such as tangs and particular functions, related mechanical stresses and even specific environments (Scerri, 2012; Scerri, 2013b). It is the combination of different lithic attributes and their relationship that has better defined the organization of inter-assemblage variability between North African MSA assemblages during MIS 5. This outcome emphasises the importance of refining typological classifications with statistically robust attribute approaches, based on experimental studies.

Instead of a simple correspondence between named industries and particular cultural groups, the results show that patterns of similarity between the assemblages in the study form complex technological clusters that articulate with the palaeoecology of North Africa during MIS 5. The particular correspondence of archaeological and palaeoecological data demonstrated in our results shows how ancient populations were organized in North Africa after environmental amelioration opened up previously uninhabitable regions for dispersal. Although it may never be possible to ascertain the direction of dispersal or the origin of these population expansions (e.g. sub-Saharan Africa and/or from limited non-Saharan MIS 6 refuges within North Africa itself), the geographic structure of the technological and ecological results is consistent with a metapopulation structure, in which partially separated populations of modern humans interacted at some level.

Specifically, the geographic structure of the degrees of technological difference identified in the results is consistent with the successive dispersal of relatively isolated local populations across the more habitable parts of the landscape, where they innovated distinctive lithic technologies (Table 1). The fact that the similarity of the technological groups decreases with distance except when connected by palaeohydrological corridors in particular suggests the successive dispersal of local populations across the more habitable parts of the landscape, where they found comparable technological solutions to similar ecological situations. The northwest African sites in the study are located along a coastal and inland sub-humid band, but separated from the southern Sahara and the northeast by an arid and hyper-arid zone (Fig. 2). Although northeast Africa exhibits more ecological continuity with the Sahara, a large arid zone narrows the more habitable area connecting the two regions to the five rivers that cross it. The only site in the study that is located in the arid zone is Tabelbala. In historic times this town formed part of a natural corridor of oases through the desert between the Sahel and the Maghreb. During MIS 5, the site was located on a riparian corridor connecting northern and southern savannah biomes across a much more restricted desert belt (Fig. 2). Other sites located in the arid belt (Fig. 2) are located at oases featuring artesian springs or groundwater upwellings (e.g. Siwa Oasis). The Haua Fteah appears to be rather more distinctive as an assemblage and did not fully cluster with the northeast African group, although it did show some similarities with other northeast African assemblages (Tables S9–S12). These specific technological patterns appear to be mirrored by the flora and fauna of the Jebel Akhdar. For example, the region has some endemic flora, suggesting that it can act as a refuge during arid periods. However, the vast majority of the large mammals found in the Haua Fteah have their origins in sub-Saharan Africa (Klein and Scott, 1986). These animals must have dispersed across the Sahara to get to the Haua Fteah, presumably along the Nile or Serir Tibesti Rivers that provided corridors across the Sahara in close proximity to the Jebel Akhdar. The distinct technological differences between the Haua Fteah and the northwest group could be explained by the fact that the two appear to be separated by a desert belt in the Gulf of Sirte that would have restricted movement of populations between the two regions (Fig. 2). These differences may also represent chronology, as the sampled assemblages may belong to the MIS 5-MIS 4 transition (Douka et al., 2014).

We argue that this 'successive budding' of populations across North Africa is more likely than an alternative hypothesis premised on cultural diffusion or blending processes. The evidence shows that most of the Sahara was hyperarid during MIS 6, indicating that most, if not all, of this vast region was uninhabited during this time (SI 1). The environmental transformation of North Africa during MIS 5 suggests a colonization of a newly available and largely empty landscape by bands of *H. sapiens* hunter-gatherers. While some contribution from blending processes is likely to have occurred, it is unlikely to represent the dominating factor in explaining the geographic relationship between the identified technological clusters.

Our results are also consistent with a number of genetic and fossil studies proposing a high degree of population structure in Pleistocene Africa prior to dispersal into Eurasia (Gunz et al., 2009; Scally and Durbin, 2012). Any population structure present in the initial range expansions of modern humans would weaken subsequent signals of growth and genetic diversity, affecting chronological estimates of genetic coalescence times between African and non-African populations (Harding and McVean, 2004). By providing insights into the character of such metapopulation structure at the gateway into Eurasia, our results have implications for refining models of early *H. sapiens* population growth, the character of dispersal out of Africa and even subsequent interactions with Eurasian archaic populations.

Finally our results provide insights into the development of dynamic and flexible technologies in the North African landscape during MIS 5, which may have had niche stabilising functions (Shea and Sisk, 2010). The highly distinctive regional nature of North African lithics during MIS 5 has been linked to identity in previous studies (d'Errico et al., 2009), however the persistence of these technologies into MIS 4 in some regions of North Africa is the strongest evidence that humans were increasingly able to construct their own ecological niches using social strategies. In this context, our results also have unexpected implications for understanding the evolution of complex culture. Sustained population structure has been linked with social trait selection, particularly the selection of cooperative behaviour (Lehmann and Rousset, 2010; Lion et al., 2011). It is also linked with a systematic underestimation of ancient population growth (Gunz et al., 2009) – an essential factor in models of the emergence of complex culture (Powell et al., 2009). The presence of complex sets of local populations using niche stabilising technologies may therefore represent an 'impossible coincidence' explaining the appearance of evidence interpreted as amongst the earliest examples for 'modern' behaviour in North Africa at ~82ka (d'Errico et al., 2009).

5. Conclusions

This study presents the first integrated analysis using archaeological, palaeoenvironmental and palaeohydrological data to explore intra-African dispersals during the Pleistocene. The results do not correlate with traditional named industries, which have been shown to be overly simplistic and based on narrow, and often somewhat subjective observations. Instead, the spatial articulation of North African palaeoecology with complex patterns of similarity between identified technological clusters shows how ancient populations were organized in North Africa after environmental amelioration opened up previously uninhabitable regions for dispersal. However, we show that not all the Sahara was environmentally ameliorated during MIS 5. The specific organization of similarities between the assemblages shows a high degree of spatial structure, such that similarities are generally the greatest either with geographic proximity or when connected by fluvial networks. While further data, particularly from ancient DNA and 'African-like' archaeological sites in regions such as the Arabian Peninsula (e.g. Groucutt and Petraglia, 2012; Scerri et al., *in press*), will provide greater clarity on these early intra-African dispersals, we have demonstrated a pronounced variability of lithics produced by early *H. sapiens* populations in North Africa during MIS 5. The significance and consistency of our results under a range of different measures suggests that the degree of subdivision between these populations was both strong and long-standing. Critically, this metapopulation structure is likely to predate dispersal out of Africa and emphasizes the importance of taking range expansions and demographic complexity within Africa into account when considering human origins.

Author contributions

E.S. led the writing of the manuscript. E.S. collected and analysed the archaeological data and developed the interpretation. R.J. created the climate model, integrated data maps and ran the spatial interpolations. N.D. contributed the hydrological data. H.S., N.D. and R.J. contributed to the writing of the manuscript. All authors discussed all results, contributed to the interpretation and commented on the manuscript.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2014.07.019.

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